Face perception in monkeys reared with no exposure to faces

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Infant monkeys were reared with no exposure to any faces for 6–24 months. Before being allowed to see a face, the monkeys showed a preference for human and monkey faces in photographs, and they discriminated human faces as well as monkey faces. After the deprivation period, the monkeys were exposed first to either human or monkey faces for a month. Soon after, the monkeys selectively discriminated the exposed species of face and showed a marked difficulty in regaining the ability to discriminate the other nonexposed species of face. These results indicate the existence of an experience-independent ability for face processing as well as an apparent sensitive period during which a broad but flexible face prototype develops into a concrete one for efficient processing of familiar faces.

deprivation | development | early experience | sensitive period

The face recognition system is capable of extremely fine within-category judgments to recognize and to discriminate between faces and the different facial expressions displayed by the same face (1, 2). To support this ability, it has been proposed that a separate system evolved to mediate face recognition (2, 3). However, the ontogeny of the face-processing system is still a matter of active debate. Researchers have argued that face processing is a special perceptual process and is organized as such at birth (4–6). In contrast, others have also argued that face processing has its origin in a more general-purpose perceptual system that becomes specialized after frequent visual experiences (7, 8).

Support for both views is found in various developmental studies. Human newborns were found to display visual preferences for face-like stimuli, suggesting experience-independent abilities (9, 10). However, patients with congenital cataracts deprived of patterned visual input for the first months of life were found to be severely impaired at discriminating faces that differed only in the spacing of their features, indicating the importance of early experience (11, 12).

To understand better the face-discrimination process, infant monkeys were reared with no exposure to faces or face-like stimuli. The monkeys were separated from their mother immediately after birth and reared separately by human caregivers. To provide a rich visual environment for the infant monkeys, their enclosures were decorated with many imitation flowers and many colorful toys. The infant monkeys, however, were prevented from seeing any faces or face-like stimuli. The human caregivers wore face masks whenever interacting with the monkeys (Fig. 1). This face-deprivation period was 6 months for four monkeys, 12 months for another four monkeys, and 24 months for a final two monkeys. The face-processing abilities of the monkeys were tested a week before, a month after, and a year after the deprivation period.

The infant monkeys were tested by using a preferential looking technique to characterize any preference for face stimuli. The stimuli were gray-scale pictures of monkey and human faces as well as nonface objects (Fig. 2). They were also tested by using the visual paired-comparison procedure (VPC) to identify whether they could discriminate between familiar and novel

Fig. 1. An infant monkey and her living circumstance. An infant monkey and a caregiver with (*A*) and without (*B*) a facemask. Both photos were taken after the face-deprivation period. (*C*) Toys placed in the monkey's home cage. (*D*) Decorations provided around the home cage.

faces. VPC indexes the relative interest in the member of a pair of visual stimuli made of one novel item and one item already seen in a prior familiarization period. Recognition is inferred from the subject's tendency to fixate on the novel stimulus significantly longer. It is important that subtle differences in the shape of specific features such as the eyes and mouth (featural information) and in their spacing (configural information) should also be encoded for face recognition (11–13). To differ-

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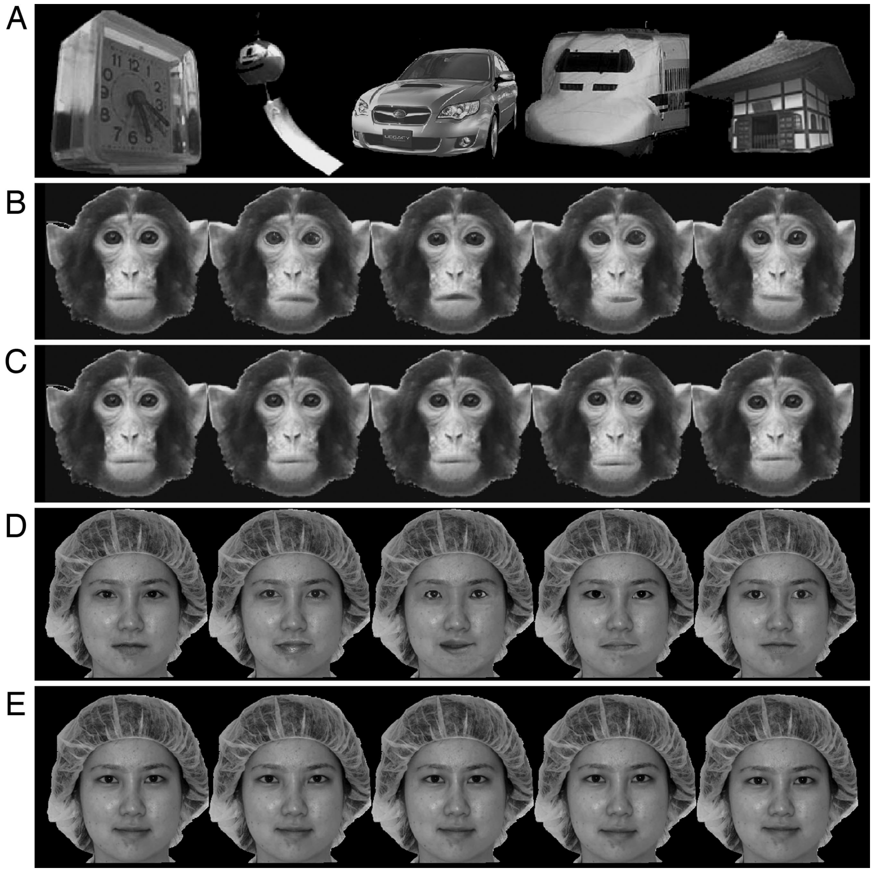

Fig. 2. Visual stimuli. (*A*) Photographs of nonface objects. (*B*) Featural stimulus set of monkey faces: variation in individual features (eyes and mouth). (*C*) Spacing stimulus set of monkey faces: variation in spacing of the eyes and between eyes and mouth. (*D*) Featural stimulus set of human faces. (*E*) Spacing stimulus set of human faces.

entiate between configural and featural processing, pairs of stimuli were created that differed only in the shape of the eyes and mouth (feature set) or only in the spacing between the internal features (spacing set).

Results

The infant monkeys showed remarkable face-processing abilities even though they were never exposed to faces or face-like stimuli.

Preferential Looking Results During the Face-Deprivation Period. As is the case for human infants (4–6), all infant monkeys showed a preference for faces. They preferred looking at both human and monkey faces. When human and monkey faces were presented simultaneously, the monkeys looked at the human faces just as long as they did at the monkey faces (Fig. 3*A*). In contrast, control animals exhibited a preference for a monkey face but not a human face. They looked at monkey faces longer than at human faces when human and monkey faces were presented simultaneously (Fig. 3*B*). The looking time at human faces was transformed into a percentage of the total looking time. The looking time at monkey faces, when paired with nonface objects, was also transformed. A repeated-measures ANOVA was performed on the looking time. A one-way ANOVA revealed that the looking time of the control animals was significantly different across the three conditions [$F(2,9) = 19.10$, $P < 0.01$]. However, a two-way ANOVA (looking condition $\times$ age) on the face-deprived infant monkeys resulted in no main effect of looking condition [$F(2,21) = 0.02$, $P > 0.5$], no main effect of age [$F(2,21) = 0.52$, $P > 0.5$], and no interaction [$F(4,21) = 0.012$, $P > 0.5$]. These results are consistent with the idea that infants possess from birth some information about the characteristics of faces (4–6).

VPC Results During the Deprivation Period. For both the featural and spacing face sets, all infant monkeys looked at novel human and monkey faces longer than at familiar human and monkey faces (Fig. 4*A*). These results indicate that all infant monkeys could discriminate between novel and familiar faces in both monkey and human face sets, even though they had not been exposed to any faces or face-like stimuli. However, control monkeys not deprived of face-like stimuli during infancy could not discriminate between novel and familiar faces from the human face set, although they could from the monkey face set. The looking time at the novel face was longer than at the familiar face, only for the monkey face stimulus but not for the human face stimulus (Fig. 4*B*). The looking time to novel faces in a pair of novel and familiar faces was transformed into a percentage of the total looking time. An ANOVA was also carried out for the percentage of the looking time. A one-way ANOVA revealed that the looking time of control animals was significantly different across the four conditions [$F(3,12) = 5.19$, $P < 0.05$]. However, the two-way ANOVA (looking condition $\times$ age) on the experimental animals resulted in no main effect of the looking condition [$F(3,28) = 0.02$, $P > 0.5$], no main effect of age [$F(2,28) = 0.01$, $P > 0.5$], and no interaction [$F(6,28) = 0.02$, $P > 0.5$].

After the Deprivation Period. After the deprivation period, the infant monkeys were kept in a separate room for a month, during which the monkeys were exposed for the first time to either

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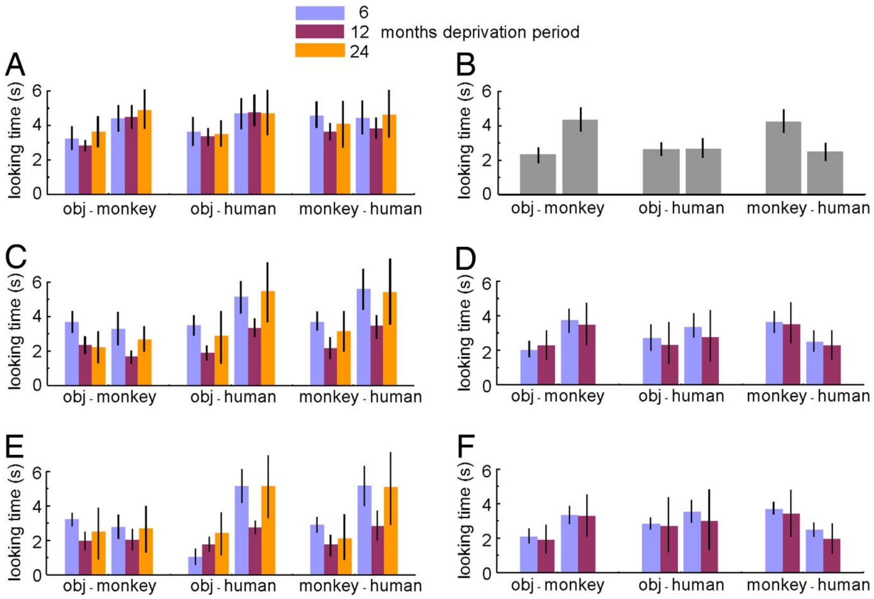

Fig. 3. Average looking time for the preferential looking task. (*A*) Results obtained during face-deprivation period. (*B*) Results from control adult monkeys. (*C*) Results obtained from the monkeys exposed to human faces for a month. (*D*) Results obtained from the monkeys exposed to monkey faces for a month. (*E* and *F*) Results obtained a year after the deprivation period from the monkeys exposed first to human faces (*E*) and to monkey faces (*F*). Error bars represent SE.

human faces or monkey faces. After this period, the infant monkeys were moved into a normal animal room. It was then found that the monkeys' preferences and recognition for monkey and human faces changed drastically.

Preferential Looking Results After the Deprivation Period. After a month of face stimuli, the monkeys exhibited a preference for facial features to which they were exposed (Fig. 3 *C* and *D*). Infant monkeys that were exposed first to human faces looked at human faces longer than at nonface objects, but they looked at monkey faces just as long as they did at the nonface objects. When human and monkey faces were presented simultaneously, the monkeys exhibited a preference for human faces. A two-way ANOVA (looking condition × age) revealed the significant main effect of the looking condition [$F(2,9) = 61.67$, $P < 0.01$], but no main effect of age [$F(2,9) = 3.24$, $P > 0.05$] and no interaction [$F(4,9) = 3.44$, $P > 0.05$] In contrast, monkeys that were exposed first to monkey faces looked at monkey faces

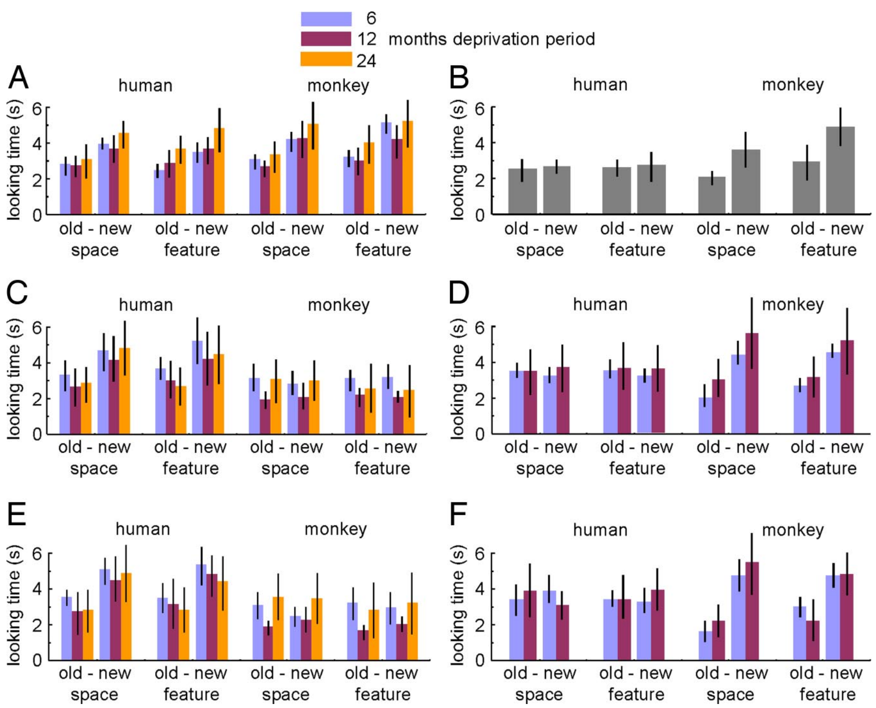

Fig. 4. Average looking time for the VPC task. (*A*) Results obtained during face-deprivation period. (*B*) Results of control adult monkeys. (*C*) Results obtained from the monkeys exposed to human faces for a month. (*D*) Results obtained from the monkeys exposed to monkey faces for a month. (*E* and *F*) Results obtained a year after the deprivation period from the monkeys exposed first to human faces (*E*) and to monkey faces (*F*). Error bars represent SE.

longer than at nonface objects, but they looked at human faces only as long as they did at nonface objects. Furthermore, when human and monkey faces were presented simultaneously, the monkeys exhibited a preference for monkey faces. A two-way ANOVA (looking condition × age) revealed the significant main effect of the looking condition [$F(2,6) = 8.40, P < 0.05$] but no main effect of age [$F(1,6) = 0.23, P > 0.05$] and no interaction [$F(2,6) = 1.88, P > 0.05$].

The preference of the monkeys did not change for at least a year after they were moved to a normal animal room, where they could see both human and monkey faces as well as interact with other monkeys (Fig. 3 *E* and *F*). The monkeys that were exposed first to human faces showed a preference for human faces [$F(2,9) = 55.45, P < 0.01$]. In contrast, the monkeys that were exposed first to monkey faces exhibited a preference for monkey faces [$F(2,6) = 12.79, P < 0.01$]. These results indicate that a preference for a particular form of face is severely shaped by early experience.

VPC Results After the Deprivation Period. VPC results also changed drastically. The monkeys that were exposed for the first time to human faces looked at novel human faces longer than familiar human faces, both for the feature and spacing face sets. However, for monkey face stimuli, they looked at the novel stimulus only as long as they did at the familiar stimulus (Fig. 4*C*). A two-way ANOVA revealed that the looking time for the novel faces was significantly different for the four conditions [$F(3,12) = 48.60, P < 0.01$]. However, there was no significant difference for deprivation periods [$F(2,12) = 2.09, P > 0.05$] or interaction [$F(6,12) = 0.86, P > 0.05$]. Of special interest was that the ability to discriminate novel and familiar monkey faces did not normalize for at least a year even after they were placed in a normal animal room (Fig. 4*E*). They looked at novel human faces significantly longer than at familiar human faces, but they looked at novel monkey faces just as long as they did at familiar monkey faces. The looking time for the novel faces was significantly different for the four conditions [$F(3,12) = 10.46, P < 0.01$].

However, the monkeys that were exposed first to monkey faces were only good at discriminating monkey faces (Fig. 4*D*). They looked at novel human faces only as long as they did at familiar human faces. However, they looked at novel monkey faces longer than at familiar monkey faces. The looking time for the novel faces was significantly different for the four conditions [$F(3,8) = 27.71, P < 0.01$]. Their ability to discriminate human faces also did not normalize for at least a year (Fig. 4*F*). They looked at novel human faces just as long as they did at familiar human faces, but they looked at novel monkey faces longer than at familiar monkey faces. The looking time for the novel faces was significantly different for the four conditions [$F(3,8) = 14.84, P < 0.01$].

Discussion

The present experiments examined how monkeys not exposed to any faces or face-like stimuli after birth process faces. Sackett (14) reared monkeys in isolation from birth to 9 months and provided visual input using only photographs. He suggested that socially meaningful stimuli (i.e., pictures of a threatening monkey and pictures of infants) may have prepotent and activating properties for socially naive infant monkeys. In the present work, the infant monkeys showed remarkable pattern-processing abilities for face stimuli, even though they had never seen any faces. They could recognize and discriminate faces on the basis of configural as well as local information.

The infant monkeys that were not previously shown facial stimuli of any kind exhibited a preference for both photographs of monkey and human faces, indicating that face detection is protected against interfering nonface objects at least for 2 years. These results seems to be consistent with the hypothesis that newborns are able to detect the basic interrelated features of the face, for example, two eyes above a nose and a mouth below the nose (15). However, there is ample of evidence that genetic factors are always part and parcel of the individual organism's entire developmental system (16). The infant monkeys would learn that they move their eyes when they look at objects and move their mouth when they eat. Furthermore, they rubbed their own face with their hands and sucked their fingers very frequently. It is very likely that the infant monkeys acquire the knowledge about the interrelated features of the face through proprioceptive and tactile information. Therefore, facial structure might become a familiar and attractive visual object without the experience of the face itself.

The infant monkeys could discriminate photographs of familiar and unfamiliar faces both for the spacing and featural face sets, even though they were never exposed to faces or face-like stimuli. In human developmental literature, it was shown that configural face processing develops slower than featural processing (17). At 7 months, human infants are able to process the relationship among the parts of a face (18), but even 10-year-olds made more errors than adults in discriminating faces on the basis of configural information (17). However, the difference in the developmental time course of configural and featural face processing was not observed in the present work. Rather, the present results indicate that the infant monkeys are able to recognize the spacing between facial features without experience. These experience-independent abilities are retained without deterioration for at least 2 years. Exposure to faces *per se* may not be necessary for the development of configural face-processing abilities.

The development of featural and configural processing is not limited to face perception. Both processing abilities can be observed with nonface pattern processing in human infants (19–22). It has been shown that response properties of cells in 4-month-old monkey inferior temporal cortex are very similar to those of adult monkeys (23, 24). It is therefore very likely that both featural and configural pattern processing develops without experience of faces. The infant monkeys can process faces using both processing mode when they see faces for the first time.

The ability to recognize individual group members and the corresponding relationships is an important and necessary part of the social lives of primates (25). After exposure to human or monkey faces, the face-processing abilities of the infant monkeys changed drastically. The monkeys started to exhibit a preference for the species of face to which they were initially exposed. Furthermore, they selectively discriminated the exposed species of face. These results indicate that the well known "other-race effect" (26, 27) and "other-species effect" (28) may be caused by frequent exposure of subjects during infancy to the prototypical facial environment. The development of the face processing of one's own species through experience with faces of conspecifics has been also demonstrated in other primates (29, 30). In human developmental studies, it was shown that, although 3-month-old human infants discriminate and recognize only own-race faces, a short training with other-race faces cancels this other-race effect (31). Furthermore, Asian children reared with exclusively Asian people adopted in European families in Europe between the age of 5 and 9 years, showed the same own-race effect as European subjects when they grew up to be adults (32). It was also shown that exposure of 6- to 9-month-old human infants to monkey faces prevents the other-species effect (33). The other-race effect and the other-species effect are, therefore, not stable in human infants. The reversibility and plasticity questions of the other-species effect in monkeys remain to be answered.

The present results are consistent with the concept of perceptual narrowing, that is, selective experiences with familiar stimuli lead to a decline in the ability to recognize other

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unfamiliar stimuli (32, 34, 35). In addition, the results indicate the existence of a sensitive period for face perception, where specific experiences gained over a short period significantly affect later development. During this sensitive period, socially meaningful visual stimuli that respond to the infant's behavior attract the infant's attention and play an important role in developing a face prototype into a concrete one for efficient processing of familiar faces. However, the duration of this sensitive period is not simply related to the period after birth. The present results indicate that the face-sensitive period can be extended for at least 2 years if infant monkeys are never exposed to face stimuli. Face deprivation, therefore, seems to delay the normal maturation and keeps the face-processing system in an immature state, as has been demonstrated in the primary visual cortex that visual deprivation such as dark rearing prolongs the critical period for ocular dominance plasticity (36, 37).

Materials and Methods

Subjects. One 2-year-old male and three 2-year-old female Japanese monkeys (*Macaca fuscata*) were used as control animals. They were reared by their mother in an open-air monkey colony. The colony consisted of ≈30 monkeys. The experimental animals were 5 female and 5 male Japanese monkeys. They were separated from their mother within few hours after birth, when these births occurred during daylight hours. For night births, the newborn infants were separated from their mother before 8 o'clock the next morning. The infants were reared by human caregivers in a separate room and provided with many items such as imitation flowers. The monkeys were also given many colorful toys to play with in their home cages. They also played with caregivers for at least 2 h per day. Caregivers always wore face masks whenever interacting with the infant monkeys. One month before the end of the face-deprivation period, the infant monkeys were trained to sit down on a monkey chair and were rewarded with a drop of fruit juice when they kept looking at the front screen (50 cm wide and 30 cm high) for 5 s. During the training and test phases, the monkeys could drink water freely in their home cages for an hour after daily sessions.

After the deprivation period, infants were kept in the separate room for a month, during which time they were exposed for the first time to either human faces or monkey faces, for a month. Two of the 6-month-old and 12-month-old monkeys were exposed to monkey faces, respectively. Each of them was caged with another monkey, so that they could interact. The remaining six monkeys were exposed to human faces. Their caregivers did not wear face masks and interacted with them for at least 2 h per day. One month after the deprivation period, experimental animals were caged in pairs and placed in a room with at least 10 other monkeys in other cages.

All experimental procedures were approved by the Institutional Animal Use and Care Committee of the National Institute of Advanced Industrial Science and Technology.

Visual Stimuli. Gray-scale digitized full-frontal images of 20 human and 20 monkey faces were prepared. From these images five human and five monkey faces were selected to create eight new versions (13). The four modified faces in the featural set were created by replacing the eyes and mouth with the features of the same length from different humans or monkeys. The two modified faces in the spacing set were created by moving the eyes up and the mouth down, or the eyes down and the mouth up, compared with the original, so that the distance between the eyes and the mouth was lengthened or shortened by 6%. Another two modified faces in the spacing set were created by moving the eyes closer together or further apart by 6%. Twenty images of nonface objects, such as houses, household objects, and vehicles were also prepared. The experimental animals had never seen these objects in any form. All stimuli were back-projected on to a ground-glass screen. Mean luminous intensity and peak-to-peak contrast of each image were ≈70.0 cd/m^2 and ≈140, respectively.

Preferential Looking. The monkeys were seated in front of the screen. The stimuli were gray-scale pictures of faces and nonface objects. A stimulus pair was randomly selected from three different pairs of stimulus categories (human face–nonface object, monkey face–nonface object, and human face–monkey face). Two pictures (10 × 10 cm each; the distance between the centers of the two pictures was 30 cm; the viewing distance was 60 cm) were also randomly selected and presented side by side on the screen. The side of the two stimuli (left or right) was randomized and counterbalanced across subjects. At the center of the screen, a flickering red circle (1° in diameter) was used to attract the monkey's attention. The circle blinked at a 333-ms on/off cycle. Video cameras were placed just below two stimuli and the center of the screen, respectively. Each trial began with flickering the center circle. As soon as the monkey fixated on the light, the flickering circle was turned off and the two stimuli appeared simultaneously for 10 s. Videotapes of the monkey's eye movements throughout the 10-s trial were subsequently analyzed by two observers who were blind to the conditions and who judged, frame by frame, whether the subject was looking toward the right screen, the left screen, or away from both (interobserver agreement was 0.94, as measured by Pearson's correlation). The intertrial interval (ITI) was 10 s. Ten video recordings were obtained for each condition. A total of 30 recordings were carried out within 30 min.

Visual Paired Comparison. A VPC task was performed the day after the preference test. A procedure similar to the preferential looking test was used. However, in the VPC task, the animals were first presented with a face stimulus projected onto the screen center. The stimulus duration was 5 s and repeatedly presented six times with stimulus onset asynchrony of 10 s. After a 5-s retention period, the familiar face stimulus and a new face stimulus were projected side by side from one 10-s retention test. The positions of the familiar and novel stimulus were randomized and counterbalanced across subjects. In each trial, a stimulus was randomly selected from four types of stimulus sets (human and monkey faces × featural and spacing face sets). ITI was 20 s. Six video recordings were obtained for each condition. A total of 24 recordings were carried out within 45 min.

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